Issued January 21, 1913.

U. S. DEPARTMENT OF AGRICULTURE.

BUREAU OF PLANT INDUSTRY—BULLETIN NO. 272.

B. T. GALLOWAY, *Chief of Bureau.*

HEREDITY OF A MAIZE VARIATION.

BY

G. N. COLLINS,
Botanist, Crop Acclimatization and Adaptation Investigations.

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BUREAU OF PLANT INDUSTRY.

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., October 4, 1912.

Sir: I have the honor to transmit herewith a paper entitled "Heredity of a Maize Variation," by Mr. G. N. Collins, Botanist, Crop Acclimatization and Adaptation Investigations, and recommend its publication as Bulletin No. 272 of the series of this Bureau.

Respectfully,

Wm. A. Taylor,
Acting Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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HEREDITY OF A MAIZE VARIATION.

INTRODUCTION.

A single white ear of maize was discovered in a strain of uniformly yellow corn. The conditions under which the ear appeared and the behavior of its progeny both indicated that its occurrence was in the nature of a direct mutation and not the result of an accidental mixture of seed. The present paper is an account of the heredity of this albinistic ear.

Albinistic mutations are not uncommon in both plants and animals, and many white varieties are supposed to have originated in this way, but so far as known this is the first instance of a mutation of this kind affecting the endosperm of maize. The phenomenon is believed to be of interest, since it suggests one manner in which color diversity in maize may arise.

In maize the endosperm or the starchy portion of the seed exists in two colors, yellow and white. Although this difference in the color of the endosperm or starch may in reality be unimportant, it is, nevertheless, the mark which in the minds of most corn growers distinguishes two great classes of corn. In the corn products prepared for human food the distinction between yellow and white is fundamental and affords a most striking example of the different customs of the North and the South. In the South the use of yellow varieties of corn for human food is almost unknown, while in the North, although white varieties are widely grown, food preparations are made almost entirely from yellow corn.

ENDOSPERM COLOR IN MAIZE.

The popular discrimination between white and yellow varieties of maize for human food is not the result of mere prejudice, for there can be no doubt regarding the difference in taste between the yellow and the white preparations that are on the market. What is not clear is whether the color is necessarily associated with the taste. The characteristic taste of yellow meal, for example, may be due to the choice of varieties, and the color may be only incidental.

In the endosperm of maize the yellow color when present is always confined to the corneous or horny portion of the seed. So far as observed, the soft or starchy endosperm that occupies the center of the grain and which in flour varieties fills practically the entire seed

is always white. The yellow color when present in seeds of a soft variety is therefore confined to the thin outer layer of the translucent or horny endosperm.[1] This definite relation that exists between color and texture makes it appear not improbable that there may in reality be a similar relation between color and taste.

Though the yellow and the white varieties are constantly being mixed, there is little tendency for the color to become intermediate. Very light-yellow seeds are sometimes encountered as a result of xenia in varieties where the yellow is imperfectly dominant, but the endosperm of fixed varieties is either distinctly yellow or pure white.

One source of slight variation in the intensity of the yellow color lies in the varying amount of the horny endosperm to which the yellow color is confined. Thus, in soft varieties, although the thin layer of horny endosperm may be as dark as in horny varieties, the layer is so thin that the general appearance of the seed is comparatively light.

Tracy[2] has shown that, as a rule, the white varieties are more productive than the yellow. His conclusions are based on averages of all the varieties regarding which data could be obtained, and here again it is not perfectly clear that the color bears any casual relation to the difference in productive power. So far as known, no careful comparisons have been made between the yellow and the white strains of the same variety.

How maize came to be differentiated into yellow and white varieties is shrouded in the mystery that envelops the domestication of the plant. The only suggestion is that of Tracy,[3] who advances the idea that white varieties are in the nature of degenerations from the yellow. Both yellow and white varieties are common among the most primitive types of corn that are now being grown in the American Tropics. The remains of prehistoric ears are usually so disintegrated that it is impossible to tell whether the endosperm is yellow or white, but the writer recalls none which did not have either the pericarp or aleurone layer colored.

The inheritance of the endosperm color in maize has been made the subject of comprehensive investigations from the Mendelian point of view. In the exhaustive experiments of East and Hayes[4] it was shown that in crosses between white and yellow strains the yellow color is dominant to the white in the first xenia generation,

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[1] Yellow may also occur in the waxy endosperm of the Chinese corn. See Bulletin 161, Bureau of Plant Industry, U. S. Dept. of Agriculture, entitled "A new type of Indian corn from China."

[2] Tracy, S. M. The relation of color to yield in corn. Presidential Address at the Thirty-First Annual Meeting of the Society for the Promotion of Agricultural Science, Washington, D. C., Nov. 15, 1910.

[3] Op. cit., pp. 12–13.

[4] East, E. M. A Mendelian interpretation of variation that is apparently continuous. American Naturalist, vol. 44, February, 1910, pp. 65–82.

East, E. M., and Hayes, H. K. Inheritance in maize. Bulletin 167, Connecticut Agricultural Experiment Station, April, 1911.

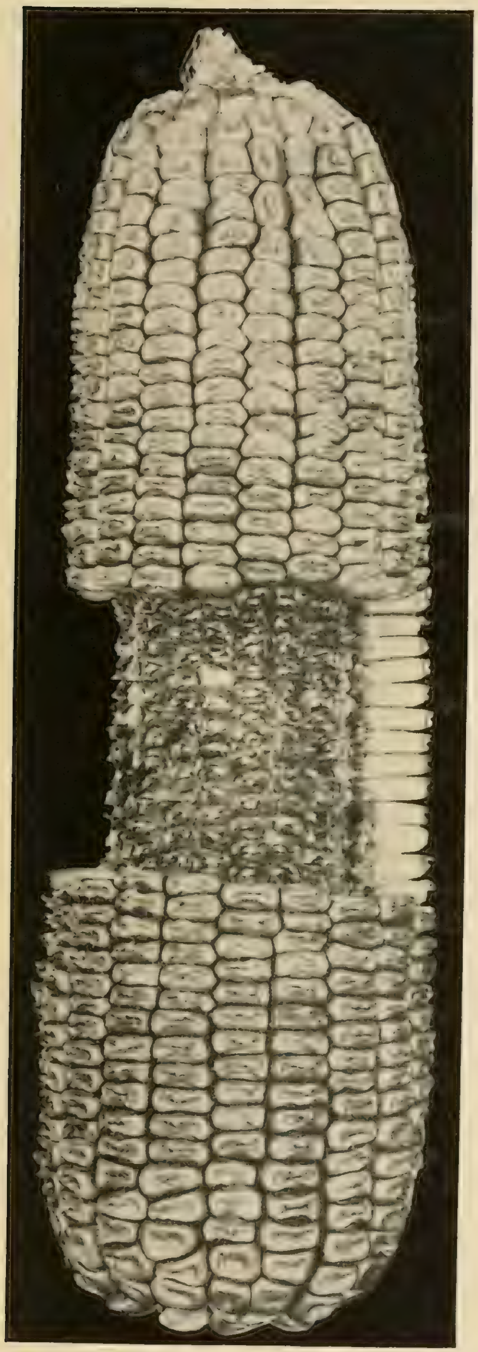

FIG. 1.—A REPRESENTATIVE EAR OF GORHAM YELLOW DENT CORN.

(Natural size.)

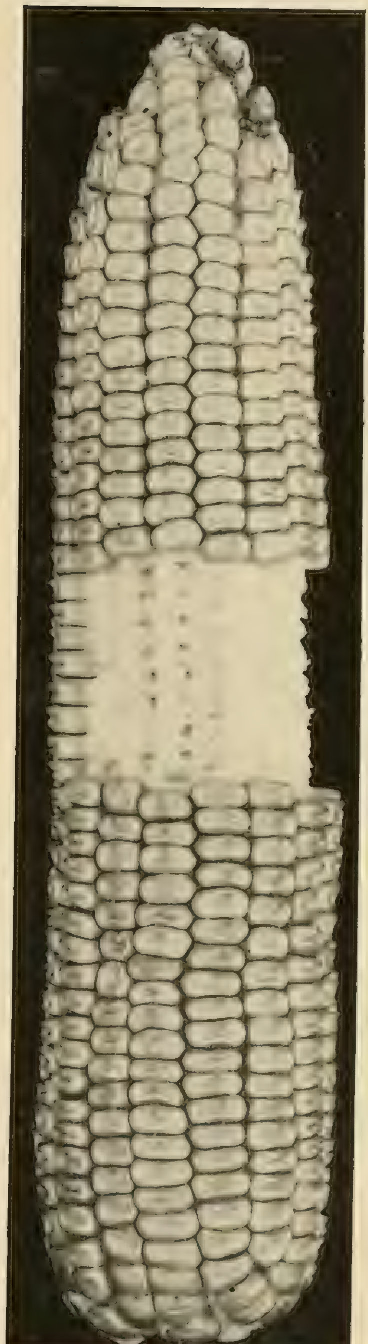

FIG. 2.—AN ALBINISTIC MUTATION FROM GORHAM YELLOW DENT CORN.

(Natural size.)

and that in the next generation the colors usually segregate in a 3 to 1 ratio. In certain crosses reported by these authors, however, the segregation was in the ratio of 15 yellow seeds to 1 white, a ratio explainable on the assumption that there are two factors or ingredients, either one of which will produce the yellow color, and that the factors are independent in inheritance.

DESCRIPTION OF THE MUTATION.

During the corn harvest of 1909 Mr. John Gorham, of Waco, Tex., observed a single white ear of a yellow-dent strain which he had selected carefully for several years. This ear came to the attention of Mr. O. F. Cook, of the Bureau of Plant Industry, who appreciated the interest of such a variation. The possibility that it might represent a mutation was recognized, and an investigation of the case was suggested.

The possibility of chance admixture of seed of a white variety seemed to be excluded, not only by the fact that the variety in which the sport appeared had been carefully selected on the place where it was being grown for a number of years but by the fact that no similar white variety was known in the neighborhood. Moreover, it appeared very strange that an all-white ear could develop in a field of yellow corn. Unless the ear had been entirely self-pollinated there should have been some yellow seeds as a result of xenia. At the same time it was apparent from differences in the shape and size of the ear that the variation did not consist merely in the loss of endosperm color. The most striking difference in form was that the kernels were much shorter than those of the yellow ears.

The Gorham Yellow Dent, the variety in which the mutation occurred, has been developed by Mr. Gorham with the assistance of Mr. D. A. Saunders. A representative ear of this variety is shown in Plate I, figure 1. The color of the seed in this variety is a rich, dark yellow. The variety, though not as uniform as some pedigree cultures, is as constant in its behavior as most commercial varieties. In the examination of the crops and in the selection of seed for six consecutive years no other color variations have been observed by either Mr. Gorham or Mr. Saunders.

A reproduction of a photograph of the white ear is shown in Plate I, figure 2. The ear was fully matured and well filled. In the original variety the cob is red; in the mutation it is pure white. The seed of the mutation, except on the closest examination, would also be considered pure white, but when carefully examined a very faint trace of yellow can be found near the base of most of the seeds. The color is much lighter than any first-generation hybrid of white and yellow that has come under observation.

It was thought that a recently acquired character, such as this colorless endosperm appeared to be, might lack the regularity in behavior that obtains with characters of longer standing and in which the expression tendencies have become more firmly established. The results have shown that the character, while Mendeloid in its inheritance, is not subject to definite and complete segregation.

PROGENY OF THE ALBINISTIC EAR.

FIRST XENIA GENERATION.

It appears probable that the plant which produced the original white ear received pollen from ordinary Gorham plants. If so, the seeds represented the first xenia generation of a cross between white and yellow in which the white was dominant or nearly so. So far as known, this is the first instance of this kind, the yellow endosperm usually being dominant to white.

Owing, perhaps, to a difference in the time of flowering, the seed of the original ear might have been self-pollinated, but in that case the self-pollinated progeny of this ear should have been all white, whereas varying percentages in the progeny showed the full yellow of the Gorham variety, giving further evidence that the ear had been cross-pollinated. It seems more reasonable, however, to associate this reversal of dominance with the appearance of a mutation where abnormal conditions may be expected to prevail rather than to assume that this unusual behavior should occur as a coincidence in connection with a single stray grain that had found its way into the seed planted in 1907. That the failure of dominance was not varietal but was largely confined to the original mutation is shown by the complete dominance of the yellow color in much of the progeny.

Seed from the original mutation was planted in 1910. One self-pollinated ear, No. 930, and two cross-pollinated ears, Nos. 741 and 721, were secured. The seed of these ears represents the second xenia generation.

SECOND XENIA GENERATION.

The self-pollinated ear, No. 930, had both white and yellow seeds, but the presence of a faint-reddish pericarp color made classification rather difficult. The appearance of a pericarp color may also be associated with the mutative change, but in the presence of the full-yellow color of the original variety this character might easily escape detection. In 1911 two hand-pollinated ears were grown from the seed of ear No. 930. One was pure white; the other contained only a few seeds, all of which had yellow endosperm.

Ear No. 741 was a cross between two plants, Nos. 82 and 47, from seed of the original ear. Ear No. 721 was the reciprocal of ear No.

741, that is, plant No. 47 was pollinated by plant No. 82. The progeny of plants Nos. 82 and 47 are shown diagrammatically in figure 1. In both ears the seeds fell naturally into two groups: Dark yellow, like the original Gorham variety, and white or very light yellow seeds. Among both the light and dark-yellow seeds were some with white caps. The white cap appears as a character independent of the color of the body of the seed, but it is difficult to distinguish in the very light-colored seeds and is here left out of consideration.

Of the two classes of seeds the dark yellow was comparatively uniform, and the second group of light-colored seeds was more

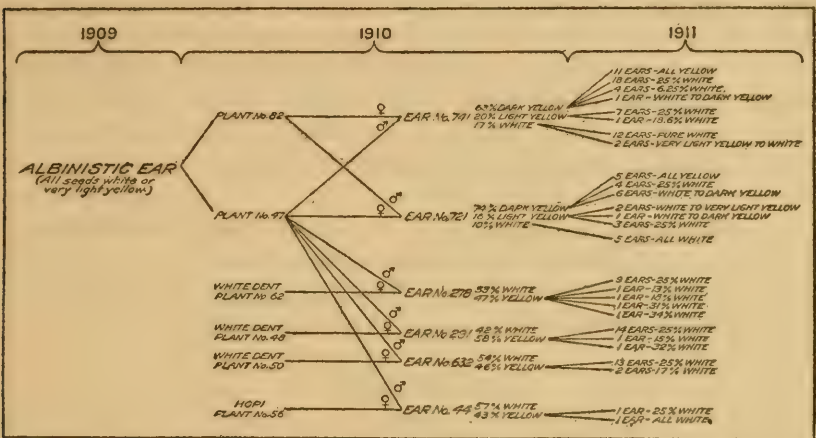

FIG. 1.—Diagram showing the inheritance of endosperm color in the progeny of an albinistic ear of corn.

variable. It was even possible further to divide the second group into white and light-yellow seeds with some degree of positiveness. Table I shows the number of seeds in the different classes.

TABLE I.—*Classification showing the number of seeds by endosperm colors in the second xenia generation.*

Ear No.	Total number of seeds.	Dark-yellow seeds.	Light-yellow seeds.	White seeds.
721	592	436	96	60
741	515	327	103	85
Total	1,107	763	199	145

Considering first the two obvious classes, dark-yellow as contrasted with the light-yellow and the white seeds, and comparing their numbers with the 3 to 1 ratio of a monohybrid, the results are shown in Table II.

TABLE II.—*Number of white seeds of the second xenia generation compared with the monohybrid ratio.*

Ear No.	Total number of seeds.	Number of white seeds.	Expected number of white seeds on a 3 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
721	592	156	148±7.1	+ 8	1.1	26.3
741	515	188	129±6.6	+59	8.9	36.5
Total	1,107	344	277±10	+67	6.7	31.1

Ear No. 721 agrees as well as could be expected with the monohybrid ratio. The reciprocal ear, No. 741, approaches more nearly the 7 to 9 ratio of a dihybrid, but from this ratio it deviates nearly five times the probable error. It is not uncommon for reciprocals to differ in endosperm color, the female parent usually exerting the greater influence. This prepotency of the female usually shows itself, however, in the intensity of the color and not, as here, in different numerical relations. No differences in the intensity of the color of the two ears were apparent.

This deviation from the normal 3 to 1 ratio is the more interesting, since the progeny of the heterozygous seeds from both these ears, which are later discussed, exhibit the same classes of dark and light yellow or white seeds, and in nearly every ear the numbers are in the ratio of 3 to 1.

Regarding the less obvious distinction between the pure-white and light-yellow seeds in these ears, it will be seen that ear No. 721 had 10.1 per cent and ear No. 741 had 16.5 per cent of the total number of seeds classed as pure white. In neither case can the ratio be referred to either the monohybrid or dihybrid ratios, which are 25 per cent and 6.25 per cent, respectively. The numbers would be approximated if we assume that one of the parent plants was heterozygous for both of two factors, either one of which would produce yellow, and that the other parent possessed only one of these factors. The expected percentage of white seeds would then be 7 to 1, or 12.5 per cent. Considered from this viewpoint the observed number shows the approximations given in Table III.

TABLE III.—*Number of pure-white seeds of the second xenia generation compared with a 7 to 1 ratio.*

Ear No.	Total number of seeds.	Number of pure-white seeds.	Expected number of white seeds on a 7 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
721	592	60	74±5.4	−14	2.6	10.1
741	515	85	64±5.1	+21	4.1	16.5
Total	1,107	145	138±7.4	+ 7	.9	13.1

It should be remarked, in connection with the excess of white seeds in ear No. 741, that out of 14 self-pollinated ears grown from the white seeds of this ear the following season 2 showed light-yellow seeds. If this ratio held, and approximately 2 out of every 14 of the ears classed as white are in reality very light yellow, the number of pure-white seeds would be reduced to 73, a deviation from the expected number of 9, or only 1.8 times the probable error.

THIRD XENIA GENERATION.

In the following year, 1911, 84 self-pollinated ears were secured from seed of the 2 reciprocal ears, Nos. 721 and 741. Sixty-four of these self-pollinated ears were from colored seeds. From the ratios secured in the second xenia generation it was suggested that one of the parents of these two ears might be heterozygous for one yellow factor, with the other factor absent, while the other parent was heterozygous for both factors. If this were true, the self-pollinated ears raised from the yellow seeds should have been colored as follows: Eighteen all yellow, 27 with 25 per cent of white seeds, and 18 with 6.25 per cent of white seeds.

In reality 15 ears were found with the seeds all yellow, 30 ears with approximately 25 per cent of white seeds, 4 ears that approximated 6.25 per cent of white seeds, and 15 ears in which the classes were either poorly marked or the number of white seeds were not referable to any expected ratio. Thus, the number of ears that were all yellow and those that had 25 per cent of the seeds white are seen to be in close accord with the expected ratios.

While in most cases the distinction between the white and yellow seeds was perfectly obvious, it did not require close scrutiny to see that the seeds placed in the white class were not uniformly pure white. This phenomenon is further discussed when the details of the different ears are given.

PROGENY OF EAR NO. 741.

Ear No. 741, which resulted from crossing 2 plants from seed of the original albinistic ear, had 515 seeds that were classified as white, light yellow, and dark yellow. Each class was planted separately in 1911.

White seeds.—Fourteen self-pollinated ears from the white seeds of No. 741 gave 12 pure-white ears; the remaining 2 ears, Nos. 770 and 779, were at first passed for white, but a close examination showed some seed with a distinct yellow tinge and many with an appreciable trace of yellow. An attempt was made to classify ear No. 779, which resulted in 368 white seeds and 128 seeds in which a trace of yellow could be seen. The classification was, however, more or less arbitrary.

Light-yellow seeds.—From the light-yellow seeds of ear No. 741, ten self-pollinated ears were secured. In two of these ears the endosperm color was obscured by a colored pericarp, and no attempt was made to classify the seed, though it could be seen that both yellow and white endosperm were represented. Of the eight remaining ears, seven showed light-yellow and white seeds in the proportion of three yellow to one white. The greatest deviation in any of the seven ears was only 2.3 times the probable error, and of the seven ears three deviated less and four more than the probable error. The total number of seeds from the seven ears was 3,193, of which 812 were white, the expected number being 798 ± 16.5, a deviation of 14 seeds, or 0.85 of the probable error.

In the remaining ear, No. 815, though also possessed of a light pericarp color, the seeds could be readily classified. The total number of seeds in this ear was 388, of which 72, or 18.6 per cent, were white. No. 815 was the only ear grown from the light-yellow seed that produced yellow seeds as dark as the yellow of the original Gorham variety. In the others the color resembled the immediate parent seed in intensity.

Dark-yellow seeds.—From the dark-yellow seeds of ear No. 741, thirty-four self-pollinated ears were secured. These were readily classified into the following groups: Eleven all-yellow ears of varying shades; 18 yellow and white ears, approximating a 3 to 1 ratio; 4 yellow and white ears, approximating a 15 to 1 ratio; and 1 ear with seeds of all shades from white to dark yellow.

The 18 ears referred to the 3 to 1 ratio are all in close agreement with the expected numbers. The total number of seeds for the 18 ears was 9,004, of which 2,281 were white, a deviation of 29 from the expected number, 2,252. There were 11 plus and 6 minus deviations. In 8 of the ears the deviation was less than the probable error; the widest deviation was 3.7 times the probable error. In every ear referred to this group the classes were well marked. In 10 of the 18 ears, however, the white class contained seeds in which a trace of yellow could be made out, but in none was there any evidence of discontinuity within the class.

In the group of four ears referred to the 15 to 1 ratio there was also an obvious gap between the dark and light-yellow seeds, though the distinction was not as pronounced as in the first group. But in these ears it was possible to separate the light seeds into light yellow and pure white with some degree of certainty, and it is this class of pure-white seeds that approximates the 6.25 per cent, or 1 to 15 ratio. The numbers for the four ears referred to this group are shown in Table IV.

TABLE IV.—*Number of seeds by seed classes in third xenia generation compared with the dihybrid ratio.*

Ear No.	Total number of seeds.	Number of light-yellow seeds.	Number of white seeds.	Expected number of white seeds on a 15 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
790	741	142	47	46±4.4	+ 1	0.2	6.3
791	557	122	17	35±3.8	−18	4.7	3.1
797	770	121	56	48±4.5	+ 8	1.8	7.3
802	657	112	57	41±4.2	+16	3.8	8.7
Total	2,725	497	177	170±8.5	+ 7	.8	6.5

In Table V the white and the light-yellow seeds are considered as one class contrasted with the dark-yellow seeds, and the numbers are compared with a 3 to 1 ratio.

TABLE V.—*Number of seeds by seed classes in third xenia generation compared with the monohybrid ratio.*

Ear No.	Total number of seeds.	Number of white and light-yellow seeds.	Expected number on a 3 to 1 ratio.	Deviation from expected number of white and light-yellow seeds.	Deviation divided by probable error.	Percentage of white and light-yellow seeds.
790	741	189	185± 7.9	+ 4	0.5	25.5
791	557	139	139± 6.9	0.0	.0	25.0
797	770	177	193± 8.1	−16	2.0	23.0
802	657	169	164± 7.5	+ 5	.7	25.7
Total	2,725	674	681±15.2	− 7	.5	24.7

Too much significance should not be attached to the ratios represented by the pure-white seeds in these four ears, though the closeness to 6.25 per cent, which is the expected percentage where two factors are involved, is suggestive. In nearly every ear the classification was more or less arbitrary. Granted that subsequent generations show that 6.25 per cent of the seeds fail to produce yellow, rather violent assumptions are necessary to account for the definite class representing 25 per cent of the total number. It would be necessary to assume that the two factors for yellow show very different potencies, so that one of them, although received from both parents, produces a much lighter yellow than where the other factor is received from only one parent. In Mendelian terminology one of the factors, "Y," for example, must be assumed to be much less effective than "Y_1", so that the classes yyy_1y_1, Yyy_1y_1, and YYy_1y_1 will be either white or very light yellow, while all other combinations are dark yellow.

Although the 25 per cent ratio is that of a simple Mendelian character, it can not be explained as such, since the recessive class

may be expected, as in the previous generation, to produce both yellow and white. A less complicated way of looking at these results is to admit the incompleteness of segregation, the group of 25 per cent representing the class in which the character fails to come into expression except in an incomplete way.

PROGENY OF EAR NO. 721.

The seeds of ear No. 721, the reciprocal of ear No. 741, were in like manner classified into white, light yellow, and dark yellow, and each planted separately. The results were in general similar to those secured from ear No. 741, except that in none of the ears could the light seeds be separated into light yellow and pure white with any degree of certainty.

White seeds.—Five self-pollinated ears were secured from the white seeds of ear No. 721. All were pure white.

Light-yellow seeds.—From the seeds that were light yellow six self-pollinated ears were obtained. Two of these ears would be passed for pure white except on very close inspection, when a trace of yellow could be made out in many of the seeds. No attempt was made to classify these ears. The classes in the remaining four ears are shown in Table VI, where the results are compared with those expected if the character was segregating as a monohybrid.

TABLE VI.—*Number of seeds, by seed classes, in third xenia generation compared with the monohybrid ratio.*

Ear No.	Total number of seeds.	Number of white seeds.	Expected number of white seeds on a 3 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
760	790	213	198±8.2	+51	1.8	27.0
763	585	280	146±7.1	+134	18.8	47.9
764	559	131	140±6.9	−9	1.3	23.4
766	69	20	17±2.4	+3	1.2	29.0

The foregoing classification was that into which the seeds could be most naturally divided, though the classes were only moderately well marked. In each ear it could be seen that some of the seeds classed as white contained minute traces of yellow. No special significance should be attached to the large number of white seeds in ear No. 763. The classes in this ear were very poorly defined, the gradations in color forming almost a continuous series from white to dark yellow.

Dark-yellow seeds.—From the dark-yellow seeds of ear No. 721 15 self-pollinated ears were secured, as follows: 5 with all-yellow seeds of varying shades; 4 with yellow and white seeds, approximating a 3 to 1 ratio; and 6 with seeds of all shades from white to dark yellow.

The 4 ears which showed classes that were distinctly marked all approximated very closely the 3 to 1 ratio. The total number of seeds

was 2,644, of which 673 were white, a deviation of only 12 from the expected 661 seeds. But in 3 of the 4 ears faint traces of yellow were apparent in seeds of the white class.

Considering the progeny of all the yellow seeds from ears Nos. 741 and 721 regardless of the intensity of the color, it appears that in every ear in which the classes were well marked the white class represented approximately 25 per cent of the total number of seeds.

In many of the ears the seeds classed as white were not pure white, and in a few ears these light seeds can be further divided into very light yellow and pure white, the latter class representing approximately 6.25 per cent of the total number of seeds. It will thus be seen that while the results from self-pollinating the second-generation plants are generally in numerical accord with the Mendelian expectation, segregation is apparently incomplete.

These results are in striking contrast with the behavior of the endosperm texture observed in hybrids between varieties with the ordinary endosperm and a Chinese variety with a waxy endosperm. In the latter crosses segregation of endosperm texture appeared complete, but numerical deviations from the expected ratios were of common occurrence.[1]

The appearance of classes representing both 6.25 per cent and 25 per cent of the total number of seeds would be in accord with the hypothesis that two factors were involved, were it not that both ratios occur in the same ear.

CROSS OF THE ALBINISTIC EAR WITH A WHITE DENT VARIETY.

It was suggested that the ratios observed in ears Nos. 721 and 741 of the second generation might be explained on the assumption that one of the parents of these reciprocal ears was heterozygous for two factors, the other parent possessing but one factor and this in a heterozygous condition.

If one of the parents of ears Nos. 721 and 741 was producing yellow and white gametes in equal numbers, it was undoubtedly plant No. 47, as shown by the results given below.

FIRST GENERATION.

Plant No. 47 was used to pollinate 3 ears of A4, a pure-white strain continuously pure seeded for three years. If plant No. 47 was producing yellow and white gametes in equal numbers these ears should have equal numbers of yellow and of white seeds. The results are shown in Table VII. (See also fig. 1.)

[1] Collins, G. N., and Kempton, J. H. Inheritance of waxy endosperm in hybrids of Chinese maize. Quatrième Conférence Internationale de Génétique, Paris, 1912, pp. 347–357.

TABLE VII.—*Number of white seeds of first xenia generation compared with a 1 to 1 ratio.*

Ear No.	Total number of seeds.	Number of white seeds.	Expected number of white seeds on a 1 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
278	288	154	144±5.7	+10	1.8	53.5
291	120	50	60±3.7	−10	2.7	41.6
632	154	83	77±4.2	+ 6	1.4	53.9
Total	562	287	281±8.0	+ 6	.8	51.1

These results are thus seen to bear out the assumption that plant No. 47 was heterozygous for only one factor. In the next generation, however, irregularities occurred.

SECOND GENERATION.

Progeny of ear No. 278.—Yellow seeds from ear No. 278 were planted in 1911 and 13 self-pollinated ears secured. All showed both yellow and white seeds, and with four exceptions the ratio might be referred to the expected 25 per cent. The total number of seeds was 4,867. The number expected to be white (one-fourth of the total) was 1,217±20.3. The actual number of white seeds was 1,158, a deviation of 59 seeds, 2.9 times the probable error. The results are shown in Table VIII.

TABLE VIII.—*Number of white seeds in the progeny of ear No. 278 compared with the monohybrid ratio.*

Ear No.	Total number of seeds.	Number of white seeds.	Expected number of white seeds on a 3 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
284	263	65	66± 4.7	− 1	0.2	24.7
289	101	24	25± 2.9	− 1	.3	23.8
716	107	27	26± 3.0	+ 1	.3	25.2
280	607	146	152± 7.2	− 6	.8	24.1
288	91	20	23± 2.8	− 3	1.1	22.0
279	705	164	176± 7.7	−12	1.6	23.3
281	585	158	146± 7.1	+12	1.7	27.0
717	367	80	92± 5.6	−12	2.1	21.8
286	370	105	92± 5.6	+13	2.3	28.4
*285	481	147	120± 6.4	+27	4.2	30.6
*287	185	64	46± 4.0	+18	4.5	34.6
*283	454	83	114± 6.2	−31	5.0	18.3
*282	551	75	138± 6.8	−63	9.3	13.6
Total	4,867	1,158	1,217±20.3	−59	2.9	23.8

* Exception referred to.

In all of these ears the number of seeds is large enough to make the deviations significant. In ears Nos. 282 and 283 the classes were not well marked, but both showed an excess of yellow seeds, and only those seeds in which the color was unmistakable were classed as yellow. In ears Nos. 285 and 287 the classes were well marked.

Progeny of ear No. 291.—Sixteen self-pollinated ears were secured from the yellow seeds of ear No. 291. Again, all showed both yellow and white seeds, all but two of which may be referred to the 3 to 1 ratio.

The total number of seeds was 8,007. The total number of white seeds was 2,012, where 2,002 ± 26.1 were expected, a deviation of 10 seeds. The results are shown in Table IX.

TABLE IX.—*Number of white seeds in the progeny of ear No. 291 compared with the monohybrid ratio.*

Ear No.	Total number of seeds.	Number of white seeds.	Expected number of white seeds on a 3 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
674	765	189	191± 8.1	− 2	0.2	24.7
675	692	170	173± 7.7	− 3	.4	24.6
683	396	96	99± 5.8	− 3	.5	24.2
297	467	120	117± 6.3	+ 3	.5	25.7
294	616	158	154± 7.3	+ 4	.5	25.6
295	403	97	101± 5.9	− 4	.7	24.0
292	662	175	166± 7.5	+ 9	1.2	26.4
679	422	97	105± 6.0	− 8	1.3	23.0
678	633	146	158± 7.3	−12	1.6	23.1
677	644	148	161± 7.4	−13	1.8	23.0
681	262	75	66± 4.7	+ 9	1.9	28.6
293	665	182	166± 7.5	+16	2.1	27.4
684	269	80	67± 4.8	+13	2.7	29.7
685	83	31	21± 2.7	+10	3.7	37.3
*676	555	177	139± 6.9	+38	5.5	31.9
*680	473	71	118± 6.4	−47	7.4	15.0
Total	8,007	2,012	2,002±26.1	10	.4	25.1

* Exception referred to.

In this family, as in the preceding, while the original assumption is borne out by most of the ears, the exceptions can not reasonably be ascribed to chance.

In both the variant ears the classes are beautifully distinct, but in ear No. 680 some of the white seeds may contain a trace of yellow.

In ear No. 685 the percentage of white seeds is high, but the number of seeds is so small that the deviation may easily be due to chance.

Progeny of ear No. 632.—Fifteen self-pollinated ears were secured from yellow seeds of ear No. 632. Of these all except three ears approximated the expected 25 per cent white. The results are shown in Table X. The total number of seeds in the 15 ears was 8,661, of which 2,014 were white. The expected number of white seeds was 2,165 ± 27.2, a deviation of 151 seeds, or 5.6 times the probable error.

TABLE X.—*Number of white seeds in the progeny of ear No. 632 compared with the monohybrid ratio.*

Ear No.	Total number of seeds.	Number of white seeds.	Expected number of white seeds on a 3 to 1 ratio.	Deviation from expected number of white seeds.	Deviation divided by probable error.	Percentage of white seeds.
666	517	128	129± 6.6	− 1	0.2	24.8
656	472	119	118± 6.3	+ 1	.2	25.2
659	735	186	184± 7.9	+ 2	.3	25.3
669	565	144	141± 6.9	+ 3	.4	25.5
665	515	124	129± 6.6	− 5	.8	24.1
667	751	181	188± 8.0	− 7	.9	24.1
672	577	150	144± 7.0	+ 6	.9	26.0
658	541	144	135± 6.8	+ 9	1.3	26.6
655	585	159	146± 7.1	+ 13	1.8	27.2
668	562	127	140± 6.9	− 13	1.9	22.6
671	609	138	152± 7.2	− 14	1.9	22.7
673	453	95	113± 6.2	− 18	2.9	21.0
*657	537	108	134± 6.8	− 26	3.8	20.1
*654	622	106	155± 7.3	− 49	6.7	17.1
*670	620	105	155± 7.3	− 50	6.9	16.9
Total	8,661	2,014	2,165±27.2	−151	5.6	23.2

* Exception referred to.

Excluding the 3 ears which do not approximate the 3 to 1 ratio, the deviation is only 25 seeds, with a probable error of 24.2.

The total progeny of the 3 ears, Nos. 278, 291, and 632, consisted of 44 ears with 21,535 seeds; of these 5,184 were white. If behaving as a simple character we should have expected 5,384±43 white seeds. Thus there is a deviation of 200 seeds, or 4.7 times the probable error. But this deviation results from the behavior of a comparatively few aberrant ears and not from a general tendency, or skew, such as was found with the inheritance of the endosperm texture.[1]

CROSS OF THE ALBINISTIC EAR WITH THE HOPI VARIETY.

In 1909 pollen from plant No. 47, the same plant that was used as the male parent in the crosses referred to in Table I, was used on a plant of the Hopi white-seeded variety, producing an ear, No. 44, having 249 white and 191 yellow seeds, with the classes very well marked. The expected number of white seeds on a 1 to 1 ratio is 220±7.1. There is thus a deviation of 4.1 times the probable error. It may be noted that the expected number of seeds on a 7 to 9 ratio is 193, but to judge from the behavior of this color elsewhere the larger class should have been the yellow instead of the white.

Three selfed ears from the yellow seeds of ear No. 44 gave in 1911 1 poorly developed yellow-and-white ear, 1 ear with 188 white and 565 yellow seeds, and *1 pure-white ear.*

The appearance of a pure-white self-pollinated ear from a yellow seed must be taken as an example of complete reversal of dominance

[1] Collins, G. N., and Kempton, J. H. Inheritance of waxy endosperm in hybrids of Chinese maize. Quatrième Conférence Internationale de Génétique, Paris, 1912.

in the parent seed or the complete loss of a Mendelian character, perhaps in the same way that endosperm color was lost in the original albinistic mutation. With the idea that the alternative characters are a function of expression it is to be expected that yellow may again appear in the progeny of this ear. The seed for the 1911 experiment was planted by the writer, and the classes of the original ear are so well marked that the chance planting of a white seed among the yellow seeds is very improbable. The progeny of this pure-white ear will be carefully watched for the appearance of yellow. The ear is well filled and fully matured and the closest scrutiny fails to disclose the least trace of yellow endosperm.[1]

DISCUSSION OF RESULTS.

Viewed in a general way it can be said that pure-seed progenies of the albinistic ear have resulted in all shades of yellow from the merest trace to the fully developed orange of the variety from which the mutation originated. The pronounced tendency for the seeds to fall into two groups representing 25 per cent and 75 per cent of the total number shows that the inheritance is Mendeloid, though not definitely alternative. The grouping into classes representing 25 per cent and 75 per cent suggests that a single character with somewhat variable dominance is involved, but on this assumption the segregation must be held to be incomplete, since the recessive class shows definite traces of yellow.

The appearance in some of the ears of a class apparently pure white, representing approximately 6.25 per cent, suggests that two factors are involved. But if two factors are involved, the definite class representing 25 per cent of the seed in the same ears that show the pure-white class of 6.25 per cent can be explained on the factor hypothesis only by elaborate and unwarranted assumptions.

The small class constituting 6.25 per cent also argues against the presence of more than two factors. For if three or more factors are involved the same violent assumptions are required to accommodate the 6.25 per cent ratio that are required to accommodate the 25 per cent ratio with two factors.

The definiteness with which the two classes represent 25 and 75 per cent is merely an addition to the large mass of evidence already on record with respect to a great variety of plants and animals, to the effect that alternative characters tend to segregate in equal numbers.

The more significant fact from the theoretical point of view is that while the segregation is usually numerically exact, it is by no means

[1] Since this bulletin was sent forward for publication the 1912 crop has been harvested. Nine self-pollinated ears from the seed of this pure white ear were secured. Five of these are pure white. All of the others have some seeds that are unmistakably yellow, though the color is faint.

complete; that is, the dominant character, yellow endosperm in this case, is not completely absent from individuals of the recessive class. This is shown not only by the presence of a faint-yellow color in most of the seeds, but also by the fact that apparently pure-white seeds from an ear in which the classes were well marked may produce seed with a fully developed yellow color when self-pollinated.

The results appear as evidence against the idea of gametic purity and alternative inheritance, but are rather in accord with the modifications of the Mendelian theory that have been advanced by Castle,[1] Reid,[2] Cook,[3] and others. These authors, while holding diverse views in many particulars, all agree that segregation is incomplete in the sense that the extracted dominants and recessives transmit traces of the alternative character in more or less latent form.

The mathematical regularity exhibited in the expression of most alternative characters is so striking and attractive that careful comparisons between the original and extracted types are often overlooked. There may have been a tendency to assume that if the characters segregated in accordance with an expected ratio the segregates were necessarily pure. The numerous examples where this has now been shown not to be the case should call for a careful reexamination of the classes in the various Mendelian experiments with this point in mind. That large numbers of individuals bred from the extracted types fail to bring the alternative characters into full expression can no longer be taken to prove that the types are "pure."

CONCLUSIONS.

The present paper is a study of the inheritance of one of the endosperm characters of maize in the progeny of an albinistic mutation. The results are of interest in relation to one of the general problems of heredity—the segregation of characters in the offspring of hybrids.

It has been assumed that alternative characters when brought together in hybrids will separate and reappear in pure form, unchanged by the temporary union. The endosperm characters of maize afford excellent material for the study of this question and have played an important part in establishing the theory of complete segregation. The numerical regularity with which many characters reappear in the later generations of a hybrid is one of the chief arguments for the theory of segregation or alternative transmission.

The results here reported of the inheritance of an albinistic variation seem to demonstrate that in this instance, while the original

[1] Castle, W. E. The inconstancy of unit characters. American Naturalist, vol. 46, no. 546, June, 1912, p. 351.

[2] Reid, G. A. O'B. The Laws of Heredity, London, 1910, pp. 159-168.

[3] Cook, O. F. Transmission inheritance distinct from expression inheritance. Science, n. s., vol. 25, June 7, 1907.

characters reappear, they are not the same; in other words, the segregation is not complete.

Previous experimenters in this field have found the endosperm color somewhat refractory as an example of the segregation theory, but by subdividing the character into factors it has been possible to bring their results into conformity with the theory. The results here reported do not lend themselves to such an explanation.

The study is based on the progeny of a white ear that appeared in a carefully selected yellow variety. The circumstances under which the variation appeared, as well as the behavior of the progeny, show that the occurrence of this white ear can not be ascribed to the accidental admixture of seed but must have arisen as an abrupt mutative change of characters.

In the original mutation the white color was almost completely dominant over the yellow. In subsequent generations, however, the yellow reappeared as a dominant character, though variable in intensity. The results accord numerically with the Mendelian expectation, but the recessive white seeds instead of being pure show minute traces of yellow.

Imperfect segregation must be taken into consideration as an obstacle to securing combinations of characters by hybridizing. The occurrence of Mendelian ratios can not be taken as conclusive evidence that subsequent selection will not be necessary to establish the full expression of characters.